III. On the Relation of Mimetic Patterns to the Original Form.* By FREDERICK A. DIXEY, M.A., M.D., F.E.S., Fellow of Wadham College, Oxford.

[Read Feb. 5th, 1896.]

PLATES III., IV., & V.

I. THE GRADUAL GROWTH OF A MIMETIC PATTERN.

It is now many years ago that Fritz Müller published an answer to those opponents of the theory of mimicry who made much of the difficulty of accounting for the first advances towards the formation of a mimetic pattern.† In the course of this communication he pointed out (as indeed Darwin had done before him) that mimicker and mimicked might, in many instances, be reasonably supposed to have started, not from a position of wide divergence from each other, but rather with the possession of some feature or features, common to them both, which should give material ready to hand for the assimilative process to work upon. The chief instance relied on by Fritz Müller in support of his contention was the well-known mimetic genus of Pierine butterflies known as Leptalis or Dismorphia. ‡ The black and yellow Leptalis (Dismorphia) melia, according to him, was to be regarded as representing the primitive type of coloration of the genus; and although it did not itself mimic any other form, it nevertheless showed independently so much of the characteristic Heliconine colours and arrangement of pattern, that the complete Heliconine aspect presented by many of its near relatives could be derived from it with comparatively slight modification.

† "Einige Worte über Leptalis," Jenaisch. Zeitschr., vol. x., 1876, p. 1.

^c A preliminary abstract of the present paper has appeared in the British Association Reports for 1894.

[†] The old genus Dismorphia has been divided by Messrs. Godman & Salvin into Dismorphia, Pseudopieris, Enantia, and Acmepteron, Biol. Centr.-Amer., Rhopal. II., p. 174. Dr. Butler further distinguishes Moschoneura, Cist. Entom., Pt. iii.

The instance chosen by Fritz Müller was unfortunate. A wider view of Pierine affinities than he had the opportunity of taking would no doubt have led him to the conclusion that, after all, the original Leptalis probably was a white or white and black butterfly, and not a black and yellow or black and orange insect like Leptalis (Dismorphia) melia. Moreover, the position that D. melia is not a mimic can hardly be sustained. It bears a very considerable resemblance to D. eumara, which is itself an almost exact copy of Actinote pellenea; Actinote being the neotropical representative of the well-known inedible genus Acrwa. There is little room to doubt that D. melia, so far from preserving the primitive Leptalis type, has diverged to some distance therefrom under the influence of mimicry.

But although Fritz Müller's principal instance does not appear to me to be strong enough to bear the weight of argument that he rests upon it, there cannot be much question that his contention in the main is perfectly sound; and that, as a general principle, the process of mimetic assimilation depends rather on the development of old, than on the starting of new features, either of

pattern or of colour.

In order to illustrate this principle, I have prepared the series of figures shown in Plates III. and IV., Figs. 1–12. These represent an array of facts that I venture to think

are in many respects of great interest.

Fig. 1 shows the underside of the male of one of the ordinary neotropical non-mimetic Pierines*, a true Pieris as that genus is restricted by Dr. Butler—P. locusta of Felder. The chief points to be observed are in the They are (1), the spots or patches of bright red which are found at the base of the precostal, median and internal spaces respectively (Fig. 1, a, c, d); (2) a well-defined yellow streak (e) occupying the costal space; (3) a pale central area (f), in many specimens yellowish, occupying the region of the cell and the adjacent portion of the wing, especially towards the internal border; (4) a dark shade (h, i) on the anal and costal sides respectively of the pale central area. The present species happens to be a rather heavily coloured member of its group, but in other species of the same genus

^{*} See below, p. 72, note.

Pieris we get a great lightening of the general tone of colour, without however losing the essential features now referred to. In P. phaloe for instance, also a nonmimetic *Pieris* from the same neotropical region, we have as it were an attenuated and washed-out version of the scheme of marking seen on the hindwing of P. locusta. Here (Fig. 2) are visible the same basal red patches, though now confined to the precostal and internal spaces; the same pale costal streak and central area, now in most specimens white rather than yellow; and on either side of the latter the same two dark shades, now reduced to a pair of brownish streaks. From either of these types to the well-known Heliconine form here represented by Heliconius numata (Fig. 11), seems a sufficiently long step; nor is it at first sight apparent that there is anything in common between the former and the latter schemes of coloration. Nevertheless, while it will be allowed on the one hand that the female of Mylothris pyrrha (Figs. 9, 10) presents a very good imitation of H. numata, it can be shown on the other hand that this last-named Pierine owes its mimetic features to a simple development of characters already possessed by the other Pierine forms just spoken of, to which it is closely allied.

In order to make this apparent, it will be necessary to refer to some of the other neotropical species of the same genus Mylothris. This interesting little group, comprising besides M. pyrrha the closely related M. malenka, M. lypera, and M. lorena, has been more than once spoken of by Mr. Wallace* as affording an instance of mimetic females associated with males of the ordinary white type of Pierine coloration. It is quite true that all the males throughout the group exhibit on their upper surfaces nothing but the ordinary white character; Mr. Wallace, however, does not mention the curious fact that the same males universally show on the under surface, though in varying degrees, an approach towards the Heliconine pattern that is so completely imitated by their mates. These partially developed features on the under surface of the males enable us to trace the history of the growth of the mimetic pattern.

Let us take the underside of the male of Mylothris

[&]quot;Tropical Nature," 1878, p. 204; "Darwinism," 1889, p. 271.

lypera (Fig. 3), and compare it with that of Pieris locusta. There is no difficulty in identifying the principal markings as before enumerated. The yellow costal streak and central area (e, f) and the anterior and posterior dark shades (h, i) are present in M. lypera as in P. locusta, all occupying the same relative positions; the precostal red however has disappeared, and the internal and median touches of the same colour have united and prolonged them. selves into a triangular streak reaching about a third of the way across the wing (cd). A small dark area (g), which in P. locusta lies immediately posterior to the internal red patch, has in M. lupera extended itself in the same direction with the extension of the patch, and has, beyond the outer extremity of the latter, united with the anterior dark area (i) in such a way as to completely surround the red patch with a distinct region of black. All the areas somewhat vaguely indicated in P. locusta have in M. lypera acquired a distinct and definite character with sharply-marked, clear-cut borders. There is no doubt of the homology of the markings in the two cases, nor does the change from one to the other deserve to be called either violent or abrupt.

The underside of the male of *M. lorena* (Fig. 4) takes us a step onward. Here are exactly the same features, but with a further development along the same lines. The red patch has now become a definite streak reaching half-way across the wing, but still bears the same relation to the anterior dark area. The costal streak and central area have undergone a similar elongation, and in this instance are much paler in colour. The whole aspect perhaps recalls that of *P. phaloe* rather than that of *P. locusta*, and the correspondence with the former insect is still further borne out by the presence of a diagonal dark streak (k) in the forewing, part of which is indicated in *P. phaloe*, uniting the costal with the posterior or

outer margin.

The general streakiness of the male of *M. lorena* is preserved or enhanced in the male of *M. pyrrha* (Fig. 5). There is in this case no diagonal dark band crossing the forewing, but the red streak of the hindwing acquires additional distinctness and importance, while the banded appearance is further increased by a slight change in the disposition of the enveloping black.

As far as the hindwing is concerned, we have now

all but reached the complete mimetic condition of *M. pyrrha* ? (Figs. 9, 10). The only thing still wanting is an infusion of more or less brownish red into the pale yellow or orange of the costal and central streaks. It is observable that even in the female *M. pyrrha* the assimilation between the old red of the basal patch and the new red of the costal and central areas is not quite perfect, the former always retaining on the under surface a more vigorous and decided tint than the latter (see

Fig. 9, e, cd, f).

With regard to the forewing, there is no doubt a considerable interval between the male and female of M. pyrrha. An inspection, however, of the female of M. lorena and M. malenka (Figs. 6, 7, 8), enables us to see how it may be bridged over. Comparing the sexes of M. lorena (Figs. 4, 6, 7), we find that their patterns are identical in the main features, though the female has an additional dark streak in the forewing (1) running parallel with the inner border. The central pale area of the hindwing has also in the female almost or entirely disappeared from the lower surface, while the other spaces on both wings which in the male are white or very pale yellow, assume in the female a deeper yellow, warming towards the base of the wing to an orange or brownish red. These changes, comparatively slight as they are, are sufficient to give the female M. lorena, a decidedly Heliconine aspect. They point out, moreover, the manner in which the still more completely Heliconine facies of M. malenka ? (Fig. 8) and M. pyrrha ? (Figs. 9, 10) may grow naturally out of the Pierine materials already noticed. A very close comparison of M. pyrrha with H. numata (Figs. 10, 11) will indeed show that the correspondence of markings is not absolutely perfect in every particular; nevertheless, the general effect is marvellously alike, and if assisted by similarity in habits and mode of flight, must be amply sufficient for all practical purposes of protection to the Mulothris.

Looking at this series as a whole, and bearing in mind that it would be possible to include other forms * which would render the gradation still easier than is shown

[•] For example, P. marana and M. lypera 9.

here, we cannot, I think, feel any doubt that it is sufficient to demonstrate the possibility of the formation of a practically perfect mimetic pattern from the ordinary form of a quite distinct type, without any violent or abrupt changes of design. It does not, indeed, lend any support to the view that mimicry can only originate between forms that already possess considerable and obvious resemblance to one another, nor does it countenance the opinion that mimetic changes are effected per saltum. What the series of forms here figured does show is that, granted a beginning however small, such as the basal red touches in the normal Pierines, an elaborate and practically perfect mimetic pattern may be evolved therefrom by simple and easy stages.

II. SEXUAL DIMORPHISM IN MIMETIC FORMS.

There remains, in regard to the foregoing series, a question of great interest; namely, what is the meaning of the diversity between the sexes in these more or less completely mimetic forms? Why should the one sex have advanced so much further along the mimetic path than the other? It is no doubt the case that the females stand in greater need of protection than the males, but to say this still leaves several questions unanswered. Are we right in regarding the male patterns as perpetuating stages through which the other sex has also passed in order to reach its present state of mimetic completeness, or are we to suppose that the selection by enemies has affected only the female sex, and that the patterns seen on the males are merely an incidental result of heredity, being, in fact, a secondary version of the female pattern transmitted in a weaker form? In either case, what has checked the further development of mimicry in the male? Is this imperfect development simply a passive result of the absence of necessity for change, or is there some active force at work preventing a further modification? It is well known that an explanation of a somewhat similar case has been sought in the principle of sexual selection; the females, it was suggested, as the more conservative sex, preferring in their mates the ancestral type of coloration of the group.* Mr. Wallace,

^{*} Belt, "Naturalist in Nicaragua," Ed. 1888, p. 385.

on the other hand, points out that in the Pierine group before us the habits of the two sexes are different; that whereas the females haunt the forest glades in company with the Heliconii, the males congregate and fly in the open with other species of white butterflies, among whom a reddish or brownish insect would be especially conspicuous, and would be very liable to experimental tasting.* This fact would seem to supply an active check on the development of the pattern in the male, but it still leaves undetermined the meaning of so much of the Heliconine colouring as does exist, and of this

Mr. Wallace has offered no explanation.

I am myself inclined to think that however much it may be to the advantage of these male forms to be taken under some circumstances for white butterflies of the ordinary kind, yet there must be times and occasionsprobably while the insect is at rest and settled—when the partial mimicry of the underside comes into play, and tends to afford protection. An instance in support of this view exists in Hesperocharis hirlanda (Fig. 12). This insect, like the males of those that have just been considered, is on the upper surface an ordinary white butterfly of the usual kind; the lower surface, however, presents an incipient mimetic pattern of a like degree of development with those of Mylothris, lorena & and M. pyrrha d. This can be no feeble reflection of a mimetic pattern complete in the female, for the sexes of H. hirlanda hardly differ; moreover H. hirlanda, with one or two other forms probably not specifically distinct from it, is the only species of its genus which shows any approach towards a mimetic coloration. The mimicry, slight as it is, must therefore, it would seem, be of some service, as otherwise it would in this case be meaningless; and if this be so with H. hirlanda, it is reasonable to suppose that whatever amount of protection such an approach to the Heliconine pattern confers, is also shared by the males of Mylothris.

A further point of interest that arises in connection with *H. hirlanda* is this—that a mimetic effect which generally resembles that of *M. pyrrha &*, is here reached by different means. *Hesperocharis*, like *Mylothris*, starts no doubt from a regular Pierine form, such as that

^{* &}quot;Tropical Nature," 1878, p. 205.

exhibited by P. phaloe; but whereas in Mylothris the main red streak of the hindwing arises from the internal and median basal red, and is central (Fig. 5, cd), in Hesperocharis it results from a development of the precostal and costal red patches, and occupies the corresponding regions of the wing (Fig. 12, a, b). The precostal red is undeveloped in Mylothris, and the median red is undeveloped in Hesperocharis. One result of this is that in the latter form the relative position of the main yellow and red streaks is reversed; notwithstanding which the general resemblance to Mylothris is considerable, and the difference would very probably remain undetected by many insectivorous animals. The present point has already been noticed by me elsewhere.* I draw attention to it here simply because it affords another illustration of the gradual growth of mimetic patterns from an original non-mimetic form.+

III. RECIPROCAL MIMICRY BETWEEN INEDIBLE FORMS.

In the previous communication to the Entomological Society[†] of which I have already made mention, I drew attention to certain facts which I am now able to illustrate by Pl. V., Figs. 13 and 14, representing the undersides of a Pierine (*Pereute leucodrosime*) and a *Heliconius* (*H. melpomene*) respectively. Both *Heliconius* and *Pereute* are, it will be seen, furnished with basal red spots, and this is the case with very many of the *Heliconii* and their

^{*} Trans. Ent. Soc. Lond., 1894, p. 286.

⁺ Throughout the foregoing remarks, P. phaloe and P. locusta &, have been spoken of as non-mimetic forms. This is undoubtedly the case with P. phaloe, but it is perhaps possible that even in P. locusta &, the underside of the hindwing may have (especially in darkly-coloured individuals) a certain mimetic value. The underside of the hindwing in P. locusta, P. cinerea and some others resembles that of Heliconius melpomene and other protected species in giving the general idea of a dark wing-area with yellow costal or precostal streak and basal red spots. The forewing of P. locusta contains a large surface of white, but this would be partly or wholly concealed in the resting position. It is true also that the yellow streak and red patches do not occupy exactly corresponding positions in the Pieris and the Heliconius; but there is abundant evidence to show that while affinity displays great respect for the exact position on the wing of any given feature of the pattern, mimicry to a large extent disregards this, and aims rather at a general similarity of effect. See the instance of Hesperocharis hirlanda above, and see also below, p. 74, note. ‡ Trans. Ent. Soc. Lond., 1894, pp. 296, etc

Pierine imitators. What is the meaning of this coincidence? The first answer that suggests itself is that it is simply an ordinary case of mimicry; the red spots belong originally to the Heliconius, and the Pierine has acquired similar spots in order to complete the mimetic picture. Two facts, however, militate against this supposition. The first is that these red patches, so far from being confined to the mimicking Pierines, are found to have a very wide distribution throughout the whole Pierine subfamily, existing not only, as we have seen, in nonmimetic neotropical forms such as Pieris locusta and P. phaloe, but in numerous old-world genera as well, reaching a great development in the Indian and Australian Delias, and having even left a relic in the common white butterflies of our own country. It would be extravagant to suppose that these widespread characters owe their origin simply to the necessity for mimicking certain South American Heliconii. Moreover, as I have elsewhere shown, such an origin for the old-world forms as this hypothesis would involve is at variance with what is known of Pierine phylogeny. The second fact is that although several Heliconii which are not the subjects of mimicry show marks of the kind, yet they are most constant, most distinct and most Pierine-like in species of Heliconius that serve as models. There must, it would seem, be a relation between the two forms which is not entirely due to mimicry by the Pierine. Are we then to say that the Heliconius is the mimic and the Pierine the model? This would appear to be going against all received ideas on the subject, and to be negatived by all that is known of the inedible qualities of Heliconius and of the ancestral coloration of the Pierines; nevertheless, with respect to the particular marks in question I believe that it comes near to the true expression of the fact, and I would suggest that the key to the difficulty is to be found in the following considerations.

It has been well shown by Fritz Müller,* whose conclusions have been followed and amplified by Meldola and Poulton, that there exist two kinds of mimetic associations—in one of which an edible form shelters itself by resemblance to another form well known to be inedible, this being the aspect of mimicry first detected and explained by Bates; while in the other a group is constituted all of whose members are inedible, and join

^{* &}quot;Kosmos," 1879, p. 100.

forces, so to speak, in order to share the dangers of experimental tasting. In the first kind it is obvious that the only imitation must be by the unprotected of the protected form: there is no force tending in the converse direction. But in the second kind it does not seem to have been sufficiently noticed that, especially if the numbers of the associated species are approximately equal, there may fairly be expected to arise a kind of give-and-take arrangement, in consequence of which two or more inedible forms may hasten the assimilative process by imitating each other. This is my reading of the case before us. There are some independent grounds* for thinking that the mimicking Pierines in this particular group of instances are not, as has been generally assumed, edible. It is therefore not unreasonable to suppose that being distasteful, like the associated Heliconii, and forming with them a company for mutual protection, they have both taken from and bestowed on them characteristic features of pattern-both sides, in fact, having undergone what I some time since ventured to call "reciprocal mimicry." I have elsewhere given more detailed reasons in support of this view; I reintroduce it here for the sake of illustrating it from those Pierine marks that have been specially under consideration.

disagreeable taste or odour.

^{*} E.g., (1) the abundance of some of the mimetic species of the same or of a closely allied genus, as Pereute charops and Euterpe tereas (testified to by Messrs. Godman and Salvin and by Fritz Müller respectively); and (2) the fact that the nearest old-world representatives of the same group, i.e., the members of the genus Delias, have all the characteristics of insects protected by a

[†] It may perhaps be objected that the resemblance between such forms as are represented in Figs. 13, 14 is not sufficiently close to warrant the supposition of mutual protection between them. To this it may be replied, that (1) the colour of the diagonal band of the forewing is probably in the living Heliconius much nearer to that of the Pereute than appears in the figure, which was taken from a specimen that had been for some years in the Hope collection. It is well known that the reds in Heliconius and Acras are especially apt to fade on keeping. (2) The resemblance may be enhanced by attitude, the figures having been drawn without any particular attention to this. (3) The brightly coloured basal marks, though occupying different relative positions in the two insects, convey the same general idea of a gently-curving, slender, white or vellow streak (belonging to the forewing in the Pereute and the hindwing in the Heliconius), beset near its base with isolated spots of vivid red, and traversing a black or dark-brown area of wing close to the body.

The same argument will apply to features similar to the above which may be seen in certain Papilioning, Nymphalinæ, Erycinidæ, and even in some moths. And I may say in passing that Fritz Müller's principle here referred to appears to me to be of much wider application than has been hitherto supposed. There exist several large groups more or less uniform in their scheme of coloration, though heterogeneous in their affinities, which it seems almost certain will in the main turn out to be cases of "inedible associations," each one possibly including a few instances of true mimicry within its borders. In deciding on the actual nature of such resemblances, it may be borne in mind that "reciprocal mimicry" constitutes good evidence of the distastefulness of all the forms between which it can be shown to occur, while the abundance or scarcity of a mimetic insect is also a valuable test of its edibility.

IV. DIVERGENT MEMBERS OF AN INEDIBLE GROUP.

The last set of figures (Pl. V., Figs. 15-18) discloses a remarkable state of things, which is of interest both in its bearing on what has been advanced in the preceding section, and also as providing a further illustration of the importance of small changes. The Papilio represented in Fig. 15 (P. zacynthus ?) is undoubtedly the model for the Pierine shown in Fig. 16 (E. tereas). These two insects form one of Bates's original instances of mimicry. But beside the latter we have another Euterpe, viz., E. bellona (Fig. 17), whose markings are, without doubt, homologous with those of its congener. E. bellona however, though so closely resembling E. tereas the mimic of P. zacynthus, itself copies, not the Papilio, but the members of a group of Heliconius of which H. erato (Fig. 18) is a good example. The bright yellow patch on the forewing of the Heliconius is very well imitated by the Pierine, and on the hindwing of the latter the crimson patch of E. tereas, etc., has been modified into a series of scarlet stripes; these being a palpable attempt to reproduce the radiating chestnut streaks of H. erato or one of its congeners. It is curious to see what slight modifications between the two species of Euterpe enable them to

imitate two such distinct insects as the *Papilio* and the *Heliconius*,*

The addition of these two forms, viz., Enterpe bellona and Heliconius erato, the former of which was perhaps not known to Bates, evidently complicates the "mimicry" question. Is the resemblance between the Heliconius and the Papilio, which certainly exists though it is not very close, accidental? But for the intermediate Pierine forms we should perhaps not have suspected any special relation between them. On the other hand, is the Heliconius the general model for all the rest? If so, P. zacynthus becomes a mimic instead of a model; while its own imitator, E. tereas, is in the curious position of mimicking a mimic, instead of going straight to the

fountain-head, i.e., the Heliconius.

In my opinion, the most satisfactory way of accounting for these complicated relations is the supposition that here we have another instance of a mimetic assemblage of the second kind—an "inedible association." The two extreme forms, viz., the Papilio and the Heliconius, which by themselves might perhaps not be sufficiently near one another to be mutually protective to any very great extent, are held together, as it were, within the limits of an inedible mimetic group, by the welding power of the intermediate Enterpes.† It is of interest in connection with what has been already advanced as to reciprocal mimicry, or the give-and-take system, in associations of this kind, that the Papilio, the Heliconius and both Pierines are furnished on the underside with basal red spots.

V. Conclusion.

It cannot, I think, be doubted that the remarkable facts touched upon in the present paper raise points of fresh interest in the great question of mimicry. The leading and binding idea in all that I have said has been

^{*} The Heliconine pattern is still further developed in the female, and on the under surface of the male of *E. bellona*, than on the upper surface of the latter sex as represented in Fig. 17.

[†] The series could be rendered still more complete by the insertion of *E. critias* and *E. bellona* Q, on the *Papilio* and *Heliconius* sides respectively of *Euterpe bellona* \mathcal{F} .

my conviction, formed after much deliberation, of the gradual and natural character of these complicated changes, and of the absence of any violent or arbitrary element in their process of development. Whether the explanations here suggested are true and adequate, can in most instances only be decided by observation in the field; and it is much to be desired that travellers and residents in countries where these and similar phenomena occur should carefully record all facts relating to the habits, postures, modes and times of flight, prevalence, seasonal occurrence and exact distribution of the various species that come under their observation.

There is also need of such experimental evidence as to the means of defence adopted by these forms as can only be satisfactorily obtained in the midst of their natural surroundings. Meanwhile, it must suffice to point out the conclusion towards which the only facts available appear to lead, while the actual verification by observation and experiment must perforce be left to those whose opportunities enable them to apply these final tests to the

subjects of enquiry.

My best thanks are due to Prof. Poulton, F.R.S., for much encouragement and many facilities for work. The figures were drawn, by his permission, from specimens in the Hope Collection at Oxford.

LIST OF SPECIES MENTIONED.

PIERINÆ.

Perente leucodrosime, Koll.

Euterpe tereas, Godt.

,, critias, Feld.

, bellona, Cram.

Mylothris pyrrha, Fabr.

,, lorena, Hew.

,, lypera, Koll.

" malenka, Hew.

Hesperocharis hirlanda, Stoll.

Pieris locusta, Feld.

,, phaloe, Godt.

,, marana, Doubl.

,, cinerea, Hew.

Dismorphia melia, Godt.

,, eumara, Doubl.

PAPILIONINÆ.

Papilio zacynthus, Fabr.

ACRÆINÆ.

Actinote pellenea, Hübn.

HELICONINÆ.

Heliconius melpomene, Linn.

,, erato, Linn.

", numata, Cram.

EXPLANATION OF PLATES III., IV., & V.

PLATE III.

Fig.	1.	Pie	ris	loc	custa	đ,	underside.
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2. P. $phaloe <math>\mathfrak{P}$,

3. Mylothris lypera &,,

4. M. lorena 3,

5. M. pyrrha &, ,,

6. M. lorena ?,

PLATE IV.

Fig. 7. Mylothris lorena 9, upperside.

8. M. malenka Q, ,,

9. M. pyrrha Q, underside.

10. M. pyrrha ♀, upperside.

11. Heliconius numata, upperside.

12. Hesperocharis hirlanda, underside.

PLATE V.

Fig. 13. Pereute leucodrosime, underside.

14. Heliconius melpomene,

15. Papilio zacynthus ♀, upperside.

16. Euterpe tereas,

17. E. bellona ♂,

18. Heliconius erato,

IN ALL THE FIGURES

a, precostal red patch on the base of the hindwing underside.

b, costal ,, ,,

e, costal light streak.

f, central pale area.

g, i, anterior dark shades.

h, posterior dark shade.

k, diagonal dark bar of forewing.

l, dark bar of forewing parallel to inner margin.